



## Review

# Species in a dynamic world: Consequences of habitat network dynamics on conservation planning

Astrid J.A. Van Teeffelen<sup>a,b,\*</sup>, Claire C. Vos<sup>c</sup>, Paul Opdam<sup>a,c</sup>

<sup>a</sup> Wageningen University, Department of Environmental Sciences, Land Use Planning Group, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

<sup>b</sup> University of Helsinki, Department of Biological and Environmental Sciences, Metapopulation Research Group, P.O. Box 65, Viikinkaari 1, FI-00014, Finland

<sup>c</sup> Wageningen UR, Alterra, Landscape Centre, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

## ARTICLE INFO

## Article history:

Received 15 August 2011

Received in revised form 25 April 2012

Accepted 6 May 2012

Available online 29 June 2012

## Keywords:

Biodiversity conservation

Disturbance

Dynamic landscapes

Habitat turnover

Metapopulation dynamics

Reserve network design

## ABSTRACT

Habitat dynamics (habitat turnover due to natural perturbations or human activity) are commonplace, particularly in intensively used landscapes. Conservation planning requires an understanding of how spatio-temporal habitat dynamics and species characteristics interact with and relate to species persistence. We conducted a systematic literature review to determine how spatial and temporal properties of habitat networks can be changed to improve species viability in dynamic landscapes. We searched for both generalities that can be interpreted as spatial planning guidelines and gaps in knowledge that limit the application in spatial planning. Seventy studies matched our inclusion criteria. From these studies, we extracted knowledge regarding the role of four spatial and five temporal network properties (e.g. network area and habitat turnover rate) for species viability. We found that improving spatial network properties often effectively counterbalances the negative effects of habitat dynamics. Furthermore, changes in several temporal properties can alleviate the impact on species viability, for example, by reducing clustering in habitat turnover events. From these findings, we formulated a first set of general qualitative guidelines for planning practices. Moreover, we identified gaps between the available and required knowledge for planning ecological networks in dynamic landscapes, thereby leading to a research priority list containing the following recommendations: (1) provide guidance regarding the effective management of network properties; (2) compare alternate management regimes and their cost-effectiveness; (3) study management regimes for a wide range of species and habitat properties. Given the continuing climate change and economic development, guiding network design—including habitat dynamics—is urgently needed.

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\* Corresponding author. Tel.: +31 317 483 473; fax: +31 317 419 000.

E-mail addresses: [astrid.vanteeffelen@wur.nl](mailto:astrid.vanteeffelen@wur.nl) (A.J.A. Van Teeffelen), [claire.vos@wur.nl](mailto:claire.vos@wur.nl) (C.C. Vos), [paul.opdam@wur.nl](mailto:paul.opdam@wur.nl) (P. Opdam).

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## 1. Introduction

During the past few decades, a large array of methods for designing and planning of reserve or ecosystem networks has been developed. The field of systematic conservation planning has arisen in response to ad-hoc, ineffective conservation efforts (Margules and Pressey, 2000; Margules and Sarkar, 2007). Gradually, the following developments were implemented: first, computational efficiency was improved significantly, and second, population dynamics were incorporated in a more realistic manner (Cabeza and Van Teeffelen, 2009; Moilanen et al., 2009). Simultaneously, in regions that contain a high degree of habitat fragmentation, spatial approaches have been developed to better embed conservation in spatial land-use planning (e.g. Jongman and Pungetti, 2004; Opdam et al., 2003). These metapopulation-based approaches aim to improve the spatial cohesion of conservation areas via network and planning concepts, with the goal of obtaining sustainable conditions for target species. Both of these approaches—the systematic conservation planning and the spatial land-use planning approaches—typically assume a static pattern of habitat patches. However, the importance of accounting for habitat dynamics *inside* conservation networks in the planning process has been emphasised (e.g. Opdam and Steingröver, 2008; Possingham et al., 2009; Pressey et al., 2007). We argue that in conservation planning, it is becoming increasingly important to account for habitat turnover (i.e. the loss of habitat in some parts of the network and habitat restoration in other parts of the landscape) for two reasons. First, and particularly in parts of the world with high land-use pressure, habitat destruction can occur inside protected areas as well. For example, in European Natura 2000 areas, this destruction is allowed for ‘imperative reasons of overriding public interest’ such as large infrastructural works. Nature conservation laws (e.g. the EU Habitats Directive) require habitat restoration to offset such impact on the conservation areas. Although guidelines for biodiversity offsets exist (e.g. Carroll et al., 2008; Cuperus et al., 1999; Ten Kate et al., 2004), a rigorous foundation in spatial ecology is still lacking (see Gordon et al., 2011). Second, due to climate change, many species are expected to lose suitable climate area, even inside protected areas (e.g. Araújo et al., 2011), and several calls for spatially adapting conservation networks to buffer the effects of climate change have been made (e.g. Hannah et al., 2007; Heller and Zavaleta, 2009; Vos et al., 2008). This initiative may require enlarging the network in some places or eliminating gaps in connectivity. Given these two developments, a quantitative understanding is required for how spatio-temporal habitat dynamics and species characteristics are related to the extinction probability of a given species. This understanding should be implemented in planning guidelines and tools to effectively reduce the negative effects of habitat turnover and maximise the benefits of habitat restoration.

To date, several quantitative planning approaches have explicitly accounted for dynamics such as environmental stochasticity, habitat loss and climate change (e.g. Cabeza, 2003; Carroll et al., 2010; Costello and Polasky, 2004; Leroux et al., 2007; Moilanen and Cabeza, 2002; Strange et al., 2006; Visconti et al., 2010b). However, most of these approaches assume that once protected, an area will remain suitable over time (but see also Carroll et al., 2010; Spring et al., 2010; Verboom et al., 2010; Visconti et al., 2010a). These studies are encouraging, but they all address different aspects, and a common scientific foundation regarding species viability in dynamic landscapes seems to be lacking.

Of course, biodiversity patterns are generally shaped by natural processes in succession, species interactions and catastrophic events such as floods and fires, and many species can adapt to these processes (e.g. Meulebrouck et al., 2007; Stelter et al., 1997; Wahlberg et al., 2002). However, these processes are likely to change as a result of climate change and land use change (Turner, 2010), and species that have adapted to more stable habitats are increasingly exposed to habitat dynamics. The interaction between landscape dynamics and species survival in the context of conservation has been studied empirically (e.g. Jäkäläniemi et al., 2006; Maes and Bonte, 2006; Petit and Burel, 1998). In addition, at the theoretical level, several studies have investigated the significance of spatio-temporal habitat turnover in population persistence (e.g. DeWoody et al., 2005; Drechsler, 2011; Johst et al., 2002; Keymer et al., 2000). A review of these studies might reveal important information regarding biodiversity conservation and spatial planning in dynamic landscapes. To the best of our knowledge, such an assessment has not been published previously. In this paper, we review and interpret the literature in accordance with the guidelines of systematic review (Centre for Evidence-Based Conservation, 2010; Pullin and Stewart, 2006). In particular, our goal is to help bridge the gap between ecological science and the practical world of planners and politicians (e.g. Opdam et al., 2002; Sutherland et al., 2004). Accordingly, we searched for generalities that can be interpreted as spatial planning guidelines and for gaps in knowledge that limit the application in spatial planning, asking the following three questions:

- 1(a). To what extent can the negative impact of habitat turnover on the viability of target species be compensated by changing the spatial properties of the network? (“*managing pattern*”). (See Section 1.1.2 for a description of network properties.)
- 1(b). Do critical thresholds follow from (1a), and if so, which thresholds?
- 2(a). Given a particular spatial network configuration, can the viability of target species be improved by changing the temporal properties of the network (i.e. the turnover regime)? (“*managing turnover*”).

- 2(b). Do critical thresholds follow from (2a), and if so, which thresholds?
- 3 If multiple temporal and spatial properties of networks can be adapted to strengthen the networks, which of these properties can be adapted more effectively and under what conditions?

### 1.1. Species in dynamic landscapes: what are the key variables?

We distinguish the following four categories of factors that determine the response of species populations to a change in habitat pattern (Fig. 1): (1) species properties such as habitat requirements, dispersal capacity and fecundity; (2) habitat properties such as habitat restoration time; (3) spatial network properties such as area and the quality and spatial distribution of a suitable habitat; and (4) temporal network properties such as the rates of habitat destruction and restoration. We consider species and habitat properties to be intrinsic properties upon which conservation plans must be built. In contrast, the spatial and temporal structures of habitat networks often result from human-driven land use and can therefore be influenced by spatial planning. Hence, in this review, we use species and habitat properties as a given starting point from which we consider the impact of changing spatial and temporal habitat patterns. To do so, we first specify what type(s) of intrinsic and network properties are relevant to consider in this context.

#### 1.1.1. Intrinsic properties

Species traits largely determine to what extent species are able to cope with habitat dynamics. For example, the potential rate of a population's growth, which is characterised by species' fecundity and longevity, is a key factor in coping with temporal variability (Altermatt et al., 2011; Bossuyt and Honnay, 2006; Verheyen et al., 2004). Long-lived species that typically have a large body size and a low rate of reproduction respond more slowly to changing conditions than small, short-lived species with a high rate of reproduction (Henle et al., 2004). Individual area requirements determine the carrying capacity of the habitat network, whereas species' dispersal capacity and barrier sensitivity influence the functional connectivity of the habitat network (Vos et al., 2001). For habitat types, the rates of restoration and natural disturbance are specific to the type of habitat. Thus, the effect of spatial and temporal network dynamics on species viability is shaped by both species and habitat properties. This effect has been confirmed by the large body of literature available regarding this subject (e.g. Bossuyt and Honnay, 2006; Clark, 1991; North et al., 2011; Parvinen and Meszena, 2009). However, these properties cannot be changed in a spatial planning process, although habitat restoration time can be influenced to some extent by management. In light of our aim, we therefore focus on the aspects that can be managed, namely the spatial and temporal properties of habitat networks.

#### 1.1.2. Network properties

The role of spatial network properties for metapopulation viability has been discussed extensively in the scientific literature. The total area, quality and connectivity of habitat networks have all been identified as important (i.e. inter-correlated) drivers of species viability in fragmented landscapes (e.g. Hanski and Gaggiotti, 2004). Together, habitat area and quality determine the network's carrying capacity for a particular species, and this capacity is related to both the potential population size and the extinction risk. Habitat connectivity is a key element for population viability in fragmented landscapes (Hanski, 1999; King and With, 2002), particularly where resource availability changes in both space and time (Thomas, 1994), and frequent extinction must be compensated by colonisation. Functional connectivity is influenced by the distance between habitat patches and by the permeability of the landscape between

these patches, both of which are scaled by a species-specific perspective (Moilanen and Hanski, 2006; Ricketts, 2001; Vos et al., 2002). For planning static habitat networks, several approaches have been developed to compensate for differences in spatial requirements between target species (see Opdam et al. (2008) for an overview). Given a certain degree of habitat turnover, it is essential to determine how the spatial pattern of the network can be adapted compared to a static situation by increasing the total amount of the habitat (*network area*), by increasing *network connectivity*, by changing the *variation in patch size* (many small patches, a few large patches, or a combination of small and large patches) or by changing the *variation in patch quality*.

Temporal network properties directly impact spatial properties, which in turn alter metapopulation viability (Fig. 1). Changes in habitat suitability over time (referred to as habitat turnover) can be specified at both the patch and network levels. At the network level, we distinguish both the *turnover proportion* (i.e. the fraction of the network that is affected at a given point in time) and the *spatial correlation in turnover* (the level of aggregation in the turnover pattern). At the patch level, the impact of a change in the habitat is described using the *turnover rate* (frequency or likelihood of turnover) and *turnover intensity* (the proportion of carrying capacity lost per patch) parameters. Turnover rate can be constant over time or can depend on particular patch properties such as time elapsed since a disturbance. We define this aspect as the '*temporal correlation*' in turnover. The local and regional components are related as follows: the product of the turnover rate and intensity determines the turnover proportion of the network. The temporal correlation in the turnover rate determines the variance in turnover proportion. Habitat turnover regimes can be characterised through the five aforementioned components. Here, we searched the literature for evidence to support the relative importance of the nine network properties on species viability.

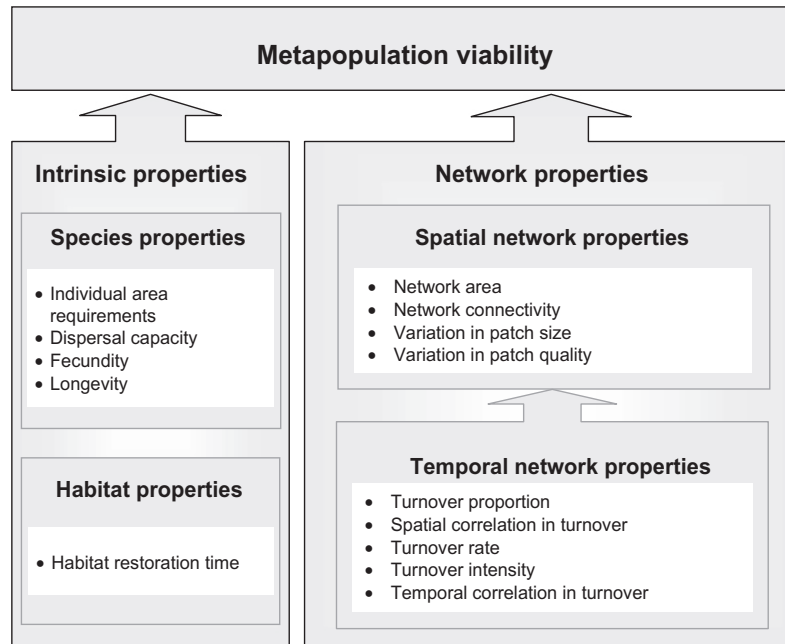
## 2. Methods

We followed the guidelines for systematic review (Centre for Evidence-Based Conservation, 2010; Pullin and Stewart, 2006) in our search strategy and data extraction methodology.

### 2.1. Search strategy, inclusion and exclusion criteria

We searched the ISI Web of Science, Scopus and Google Scholar using search terms that are associated with metapopulation viability and network dynamics (the precise search terms are listed in Table A1, Appendix A). We assessed studies for inclusion based on the title and abstract—or the full text when necessary—and included studies that matched the following criteria:

1. English language peer-reviewed papers published up to and including the year 2011 that are available as full text.
2. Studies of species viability that considered the landscape/metapopulation scale were included, whereas studies performed on a local scale only were excluded.
3. Whether the effect of network properties on species viability (or a proxy thereof) in dynamic landscapes was explicitly and systematically examined. This criterion excluded studies that:
  - a. Lacked a comparator, i.e. those studies that failed to compare an intervention (the dynamic landscape) with no intervention (i.e. a static landscape) or alternate interventions (scenarios of network dynamics). Findings from empirical studies were included in cases in which relations between network properties and (proxies for) species viability were quantified, e.g. via a statistical analysis.



**Fig. 1.** Key properties that play a role in metapopulation viability in dynamic landscapes. The network properties may be adjusted through spatial planning.

- b. Investigated only species properties; species properties cannot be changed by conservation management for which we excluded studies that aimed solely to identify (for example) optimal dispersal capacity.
- c. Solely focussed on species interactions. Thus, we focussed on the responses of individual species responses to network dynamics and consequently ignored literature related to metacommunity dynamics. Although we do acknowledge the fact that different responses of species on habitat turnover will in turn influence species interactions, including this additional dimension would have been beyond the scope of this review and would have led to incomprehensible results.

#### 2.1.1. Potential effect modifiers

In general, we expect habitat turnover to exert a negative effect on species persistence, for the following reasons: (1) habitat turnover compromises a species' ability to exploit available resources (i.e. they have to track suitable habitats); (2) disturbances that kill individuals are an additional source of extinction; and (3) because habitat loss is immediate yet habitat restoration takes time, there is a net loss of habitat area, thereby increasing the risk of metapopulation extinction. These effects apply to all species, including species that require certain levels of habitat turnover to persist over the long term (for example, because they depend on an early-successional habitat or to complete their life cycle, e.g. fire-induced seed germination). In such cases, a compromise can be expected between the benefits and downsides of network dynamics. To be explicit regarding the assumptions in the various studies, we indicated which studies included a direct benefit of habitat turnover for population viability.

#### 2.2. Data extraction

We extracted the following information from the studies that met the inclusion criteria:

- **Intervention:** Which kind(s) of regime(s) were considered (the spatial and temporal network properties mentioned in Section 1.1.2)? Did the study present empirical findings or the outcome of a model? What species (taxonomic group) were studied?

- **Outcomes:** Did interventions (measured as an increase in the network property) have a positive, negative, neutral (no effect) or mixed effect on species viability? A mixed effect was scored when a study found both positive and negative effects of an intervention on a single species (e.g. benefiting from a low habitat turnover rate but suffering from a higher turnover rate) or when different species in a single study showed contrasting responses. Were thresholds observed in these relationships, and if so, which (Questions 1 and 2)? Were alternate interventions considered, and if so, was one intervention more effective than the other (Question 3)?

### 3. Results

#### 3.1. Search results

The search strategy revealed 372 studies (see Table A1, Appendix A), of which 70 studies matched our inclusion criteria (see Tables 1 and 2 for a list of the included studies and Table A2, Appendix A for a list of excluded studies). Of these 70 studies, twelve analysed empirical data, thus covering a range of species groups (Table 1). Among the modelling studies (Table 2), 50% defined the type of species that was studied (these species were mostly plants, arthropods and mammals), and the remaining 50% did not specify what kind of species the parameter values represented. Among the studies that did not define the species, some did explain the parameter interpretations in terms of species properties such as colonisation ability or the sensitivity to stochasticity. In total, 66 studies tested temporal properties (96 disturbance treatments in total), and 32 studies tested spatial properties (51 pattern treatments in total). Twenty-nine studies tested spatial and temporal properties.

#### 3.2. Spatial network properties

We distinguished among four pattern management regimes. Of all of the spatial treatments, 86.2% exhibited a positive effect on species viability, which indicates that in general, spatial network properties can be used to compensate for habitat turnover. The evi-

**Table 1**  
 Empirical studies showing the effects of increasing the spatial or temporal network properties on species viability (or a proxy). These effects can be positive (+), negative (–), neutral (0) or mixed (±). In the study with an asterisk (\*), patch dynamics created suitable conditions for species (such as inducing germination or creating habitat).

Species group								Spatial network properties				Temporal network properties				Reference	
Plants	Arthropods	Mammals	Birds	Amphibians	Aquatic microorganisms	Other	Undefined	Network area	Network connectivity	Variation in patch size	Variation in patch quality	Turnover proportion	Spatial correlation in turnover	Turnover rate	Turnover intensity	Temporal correlation in turnover	
						×			+	+						–	Caruso et al. (2010)
						×								–			Snäll et al. (2005)
						×									–		Bushing (1997)
					×				+					±			Altermatt et al. (2011)
			×		×				+	+	+	±					Warren (1996)
		×							+	+						0	Donner et al. (2010)
	×							+			+						Magle et al. (2010)
	×										+			–			Hodgson et al. (2009b)
	×									+				–			Ranius (2007)
	×										±						Williams (2011)
×														–			Verheyen et al. (2004)
×														+		–	Menges and Quintana-Ascencio (2004)*
								1	4	4	2	0	0	1	0	0	Positive
								0	0	0	0	0	0	4	1	2	Negative
								0	0	0	1	1	0	1	0	0	Mixed
								0	0	0	0	0	0	0	0	1	Neutral
2	3	1	1	0	2	3	0	1	4	4	3	1	0	6	1	3	Total

dence base differed by regime (Tables 1 and 2), but the effects were similar between the empirical and modelling studies. Only for network size studies allowed us to determine a threshold in spatial network properties (see Section 3.2.1). Sections 3.2.1–3.2.4 show the results for individual spatial network properties.

### 3.2.1. Network area

Enlarging networks allows metapopulations to expand and is thus expected to have a positive effect on species viability in dynamic networks as well. This prediction was unanimously confirmed—all 15 studies reported a positive effect on species viability. To properly compensate for habitat dynamics, it would be valuable to determine how much larger a network must be to maintain a given level of species viability relative to a static network. Two studies have provided insight into this trade-off. Hinsch and Poethke (2007) predicted that dynamic networks must be 1.2–2.2 times larger than static networks, and Johst et al. (2011) reported that networks must be approximately 1.2–3 times as large. In both studies, the required enlargement was species-specific—the most sensitive species had a low reproduction rate and a high Allee effect (Hinsch and Poethke, 2007), or experienced low environmental stochasticity (Johst et al., 2011). Maintaining all species at their minimum viable level within a single network would require a network size that is greater than three times the size of a static network (Hinsch and Poethke, 2007). This is larger than the aforementioned factor of 2.2, as species differ in their habitat condition requirements, thereby increasing the minimum network size. McCarthy and Lindenmayer (1999) provided insight into which patches could best be enlarged and reported that adding area in proportion to patch size was the most effective strategy (i.e. enlarge large patches rather than small patches).

Based on four additional studies, we derived thresholds with respect to the fraction of suitable habitat in the landscape. Here, the thresholds of suitable habitat in the landscape ranged from 20% to 60% of the total landscape (Kallimanis et al., 2005; Keymer et al., 2000; Kun et al., 2009; Wimberly, 2006). The lower thresholds applied to landscapes in which both the habitat and turnover probabilities were randomly distributed (Kallimanis et al., 2005) or to landscapes in which the species were extremely mobile (Keymer et al., 2000). The higher thresholds applied to species that were unable to cross habitat gaps (Wimberly, 2006).

### 3.2.2. Network connectivity

Improving network connectivity is expected to facilitate the colonisation process, which would have a positive effect on the viability of species in dynamic landscapes. Fourteen out of 15 studies, including four empirical studies, support this positive effect of connectivity on species viability (Tables 1 and 2, Fig. 2). Empirical studies revealed a significant positive correlation between connectivity and colonisation probability (Caruso et al., 2010; Donner et al., 2010; Magle et al., 2010) and population density (Altermatt et al., 2011) for four species; three other species showed no significant effect. Eight out of eleven modelling studies tested the effect of network connectivity by comparing landscapes that have a compact patch arrangement to landscapes with a random patch arrangement (or a linear patch arrangement in the additional case of Vuilleumier et al. (2007)). The two remaining studies mimicked network connectivity by varying either the cost of migration (Ronce et al., 2000) or the ability of dispersers to reach other patches (Johst et al., 2011). Improving connectivity was particularly beneficial to species with a high propensity for dispersal (Johst et al., 2011). The benefits of patch clustering may depend on the scale of the disturbance regime. Kallimanis et al. (2005) found that compact networks are highly resistant to small-scale turnover but are extremely vulnerable to large-scale turnover, as the likelihood that a turnover event would impact all populations simultaneously increased.

### 3.2.3. Variation in patch size

Fourteen studies tested the effect of changing patch size distribution. The results were somewhat mixed (Fig. 2, Tables 1 and 2) because these studies addressed different questions with respect to patch size distribution. We summarise the findings according to the questions that were addressed.

Compared to static networks, dynamic networks perhaps better consist of more (albeit smaller) patches (with network area being equal). In doing so, the extinction risk due to habitat turnover would be reduced, although the extinction risk from demographic stochasticity would increase because smaller patches typically host smaller populations. With respect to static landscapes, this trade-off has been debated for decades, yielding context-dependent results (SLOSS debate, e.g. Diamond, 1975; Simberloff and Abele, 1976; Tjørve, 2010). Of the studies that were examined here, eight out of eleven, including four empirical studies, found that species viability correlates positively with patch size (Boughton and Malvadkar, 2002; Caruso et al., 2010; Donner et al., 2010; Litvaitis and Villafuerte, 1996; Magle et al., 2010; McCarthy and Lindenmayer, 2000; Ranius, 2007; Reed, 2004). The remaining three studies found that the overall benefit of larger patches disappeared under the following specific conditions: (1) if within-patch competition is stronger in large patches, large-patch systems resulted in lower population densities than small-patch systems (North and Ovaskainen, 2007); (2) if networks were sufficiently large in area, the risk of Greater Glider extinction was lower if the network was divided into multiple patches (McCarthy and Lindenmayer, 1999). The precise threshold for network size depended on the time horizon at which extinction risk was evaluated; and (3) if the network with more (albeit smaller) patches covers a larger range than the network with less (albeit larger) patches (i.e. the patch density in both networks is equal), then the first network performed better (Robert, 2009). Only when all patches were simultaneously subjected to habitat turnover due to high spatial correlation in disturbance events, networks with larger patches performed better (Robert, 2009).

Three studies investigated whether networks are better when composed of equally sized patches or when the patches are heterogeneous in size. Two of these studies found that the networks with heterogeneous patch sizes were superior (DeWoody et al., 2005; Xu et al., 2006), whereas the third study reported no effect (Boughton and Malvadkar, 2002). This latter study used stochasticity in the availability of habitat over time (i.e. the total amount of habitat fluctuated over time), a negative effect of which might have been responsible for their observed lack of an effect of patch heterogeneity. In the context of the trade-off explained above, a combination of large and small patches might be an effective strategy for reducing the risk of extinction from both demographic stochasticity and habitat turnover.

### 3.2.4. Variation in patch quality

Patches with higher quality habitats are often associated with increased population viability. With respect to dynamic networks, this association was generally confirmed by three empirical studies. First, Donner et al. (2010) found that patches of higher quality were occupied for longer periods. In a study by Williams (2011), eight out of 20 *Lepidoptera* species had a significant positive correlation with vegetation condition, whereas one species showed a significantly negative effect. Finally, Hodgson et al. (2009a) reported that improving patch quality (thereby enlarging its carrying capacity) was a somewhat feasible strategy to combat habitat dynamics.

If it is not possible to manage all patches optimally, would it be more beneficial to have a few high-quality patches or to distribute the management effort such that all of the patches are of moderate quality? The answer is likely to depend on the nature of habitat dynamics; if all patches are equally likely to be destroyed, it is

probably better to distribute the management over many patches. Having relatively few high-quality patches was beneficial in one case (North and Ovaskainen, 2007), but was not beneficial in another (Hodgson et al., 2009a). In the latter case, Hodgson et al. (2009a) compared only one scenario in which one-third of the patches were high quality with a scenario containing equal patch quality. This indicates that the precise distribution between the number of high-quality and low-quality patches might be crucial and may depend on the species in question.

McCarthy and Lindenmayer (1999, 2000) compared landscapes in which habitat quality within a patch could be heterogeneous (multiple habitat age classes) with landscapes in which each patch was of uniform quality; fire served as the disturbance regime. Having heterogeneous patch quality was favourable for species persistence, as (1) fire events no longer killed entire populations (i.e. heterogeneity was assumed to reduce turnover intensity; see also Section 3.3.4), and (2) it resulted in a more constant availability of resources within a patch over time (because different habitat age classes were affected differently by fire), thereby allowing populations to recover more quickly. This finding illustrates how the impact of (natural) disturbance regimes can be reduced via habitat heterogeneity (i.e. variations in habitat quality or type) when disturbance probability correlates with habitat quality (or type).

### 3.3. Temporal network properties

Given our hypotheses in Section 1.2.1, we expect that increasing the turnover proportion, the turnover rate or the turnover intensity will have a negative effect on metapopulation viability. Increasing the spatial correlation in turnover (i.e. a clustered turnover regime) could lead to difficulties in recolonisation of empty or new patches, as remaining populations would be located at a further relative distance than in a random turnover regime. Therefore, this scenario would be expected to have a negative effect. Clustering turnover events in time (temporal correlation) might carry the risk that at a certain point in time, much of the habitat would be affected simultaneously. This could force species to pass through a bottleneck of habitat availability, with an associated increased risk of extinction. In general, species that can respond quickly (e.g. with a strong colonising ability and/or fast reproduction) are expected to be more robust in increasing habitat turnover. Taken together, all five temporal network properties are expected to exert a negative effect on species viability in general. The results confirm this notion—approximately 74% of eligible studies that dealt with temporal network properties reported negative effects on species persistence (Fig. 2). In the following sections, we will discuss the details by property.

#### 3.3.1. Turnover proportion

Ten out of 13 studies found that increasing the proportion of the network that was subject to turnover indeed decreased species viability (Tables 1 and 2). Two studies reported that the response was species-dependent (Johst et al., 2006; Warren, 1996); specifically, pioneer species and species with high fecundity (fast growing) benefited from higher turnover in contrast to either species that depended on later successional stages or slow-growing species. This is not surprising, as early-successional species are generally better adapted to changing conditions. However, within these 13 studies, three studies reported that the species also benefitted from disturbance, and only Johst et al. (2006) found mixed responses to increasing turnover proportion. Thus, habitat turnover creates an additional extinction risk and cannot be regarded as uniformly beneficial for species that depend on disturbance events.

#### 3.3.2. Spatial correlation in turnover

Twenty-one studies investigated whether habitat loss and/or creation is distributed better over the network in a clustered or ran-

dom manner (Table 2). The majority of these studies (13) found that a clustered disturbance regime was more detrimental than a randomly distributed regime (Fig. 2). Two studies did not find a difference between correlated and uncorrelated disturbance regimes; this was either because the dispersal distance was not considered a limiting factor for the scale of the network (Meulebrouck et al., 2009) or because the *variance* in the number of fires per year was kept equal between the regimes (McCarthy and Lindenmayer, 2000). With respect to species that have severely limited dispersal capacity (requiring habitat continuity), clustered turnover regimes were more beneficial (Matlack and Leu, 2007; Wimberly, 2006); in contrast, the opposite was true for more mobile species (Wimberly, 2006). Moreover, the results of Groeneveld et al. (2008) suggest a higher probability of species persistence when fires are large than when fires are patchy; because they changed both the spatial and temporal treatments in combination, it is difficult to differentiate the effects of an individual treatment. Three studies explicitly tested the effect of creating new patches close to other patches (or populations) versus random placement (Biedermann, 2004; Cornell and Ovaskainen, 2008; Wahlberg et al., 2002); these studies found that clustering the habitat by the strategic placement of new habitat had a positive effect on species viability. This correlates with the finding that large patches are good candidates for network enlargement because it places new habitats close to existing habitats (see Section 3.2.1 and McCarthy and Lindenmayer, 1999).

#### 3.3.3. Turnover rate

Thirty out of 42 studies reported that increasing the frequency at which patches are subjected to turnover had a negative impact on the species (Tables 1 and 2). Five studies found a positive correlation with turnover (Tables 1 and 2). These were studies in which habitat turnover benefitted the species (e.g. habitat provision or seed germination). The mixed results reported in seven studies could be partially explained as follows: (1) species dispersal ability; in which species requiring continuous habitat for dispersal benefitted from a low degree of turnover when populations that were disconnected in the static landscape were connected by temporal habitat (Kun et al., 2009; Wimberly, 2006); and (2) the strength of intraspecific competition (Münkemüller and Johst, 2006). In the sole empirical study (Altermatt et al., 2011), six species exhibited decreased density in the disturbed patches relative to the undisturbed patches. Two species were more abundant in the disturbed patches than in the undisturbed patches, and these species had a higher growth rate.

A common question in disturbance ecology that relates to the interaction between disturbance frequency and intensity or proportion is as follows: Are species more viable in landscapes that have frequent yet mild/few disturbances, or are they more viable in landscapes that have rare yet intense/many disturbances? The results show a trend that is in favour of the former scenario, namely frequent yet mild/few turnover events (Hinsch and Poethke, 2007; Robert et al., 2003; Stelter et al., 1997).

#### 3.3.4. Turnover intensity

Turnover intensity refers to the fraction of a patch that is destroyed by a disturbance event. A larger destroyed fraction of the patch leads to a larger risk of population extinction. Hence, increasing turnover intensity should negatively affect metapopulation viability. This prediction is consistently supported by nine studies, including one empirical study (Tables 1 and 2).

#### 3.3.5. Temporal correlation in turnover

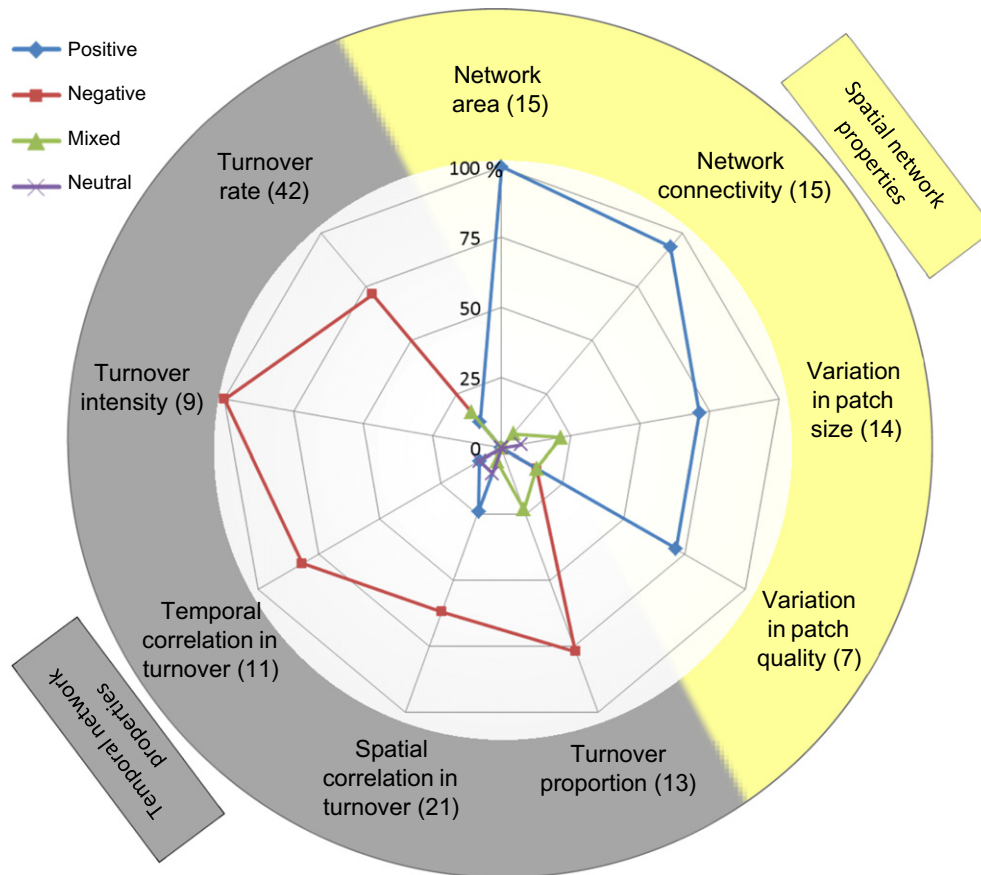
The studies in our dataset addressed different questions that are related to temporal correlation in turnover. It is therefore not feasible to sketch a general picture of the effect of temporal correlation in turnover. Below, we discuss the various questions separately:

**Table 2**  
Modelling studies showing the effects of increasing spatial or temporal network properties on species viability (or a proxy). These effects can be positive (+), negative (–), neutral (0) or mixed (±). In studies with an asterisk (\*) patch dynamics created suitable conditions for species (such as inducing germination or creating habitat).

Species group		Spatial network properties				Temporal network properties				Reference							
Plants	Arthropods	Mammals	Birds	Amphibians	Aquatic microorganisms	Other	Undefined	Network area	Network connectivity	Variation in patch size	Variation in patch quality	Turnover proportion	Spatial correlation in turnover	Turnover rate	Turnover intensity	Temporal correlation in turnover	
						×		+	±				–				Kallimanis et al. (2005)
							×	+	+			–	+				Matlack and Leu (2007)
							×	+	+				±	±			Wimberly (2006)
							×	+	+					–			Johst et al. (2011)
							×	+						±			Kun et al. (2009)
							×	+						–			Drechsler (2011)
							×	+								–	Ellner and Fussmann (2003)
						×			+	+		–					Xu et al. (2006)
							×		+				–				Johst and Drechsler (2003)
							×		+				–				Vuilleumier et al. (2007)
							×		+					–			Johst et al. (2002)
							×		+								Adler and Nuernberger (1994)
							×			±	+						North and Ovaskainen (2007)
							×			±							Robert (2009)
							×			+		–	–	–			DeWoody et al. (2005)
							×			+	0						Boughton and Malvadkar (2002)
							×					–	–				Elkin and Possingham (2008))
							×					–		–			Wilcox et al. (2006)
							×						–	±	–		Robert et al. (2003)
							×						+				Cornell and Ovaskainen (2008)*
							×							±			Münkemüller and Johst (2006)
							×							–			Best et al. (2007)
							×							–			Casagrandi and Gatto (2002)
							×							–			Keymer et al. (2000)
							×							–			Münkemüller and Johst (2007)
							×							–			Ross (2006)
							×									–	Hastings (2003)
							×									–	Johnson (2000a)
							×									–	Johnson (2000b)
						×						±					Johst et al. (2006)*
						×						–					Lundquist et al. (2010)
						×							–				Gu et al. (2002)







**Fig. 2.** The proportion of studies that reported a positive effect, negative effect, mixed effects or had no effect on species viability upon increasing a given network property. For each property, the actual number of studies that have that property is given in parentheses.

- Is it important to control for variance in turnover events? Three studies suggest that this is the case. Variance can be expressed in different ways; for example, variance may exist in the turnover rate—longer periods without turnover are alternated with shorter periods, thus leading to a given average turnover rate. Two studies concluded that variance in the turnover rate negatively affects species viability compared to a regime with a fixed turnover interval (Menges and Quintana-Ascencio, 2004; Stelter et al., 1997). Both studies investigated species that require disturbance to create suitable habitat conditions; long periods without a disturbance can lead to a critically low levels of habitat availability. Variance can also occur in turnover proportion (with more turnover in some years than in others). Such variance seems to greatly increase the risk of extinction compared to a fixed turnover proportion (McCarthy and Lindenmayer, 2000).
- What is the effect on species viability when patch turnover probability is correlated with patch age? Three studies found that species viability was decreased when the probability of patch loss was correlated positively with patch age (Hastings, 2003; Johnson, 2000a,b). Older patches are more likely to be occupied; therefore, their loss is more detrimental to metapopulation viability (Hastings, 2003; Johnson, 2000a,b). This illustrates that patch life time should exceed patch generation time. Interestingly, patch age significantly explained the population extinction risk of the prairie dog (Magle et al., 2010), but only because older patches were destroyed more frequently, not because occupied patches were significantly older than unoccupied patches (Magle et al., 2010). Moreover, in a study of lichens, Caruso et al. (2010)

found that patch destruction was correlated with patch age. However, by the time the patches were destroyed, the suitability of the patch had already decreased. As a result, populations had usually become extinct stochastically prior to the destruction of the patch, diminishing the negative effect of patch turnover. Groeneveld et al. (2008) suggested a positive effect of correlating fire probability with patch age (fuel load), but the exact signal could not be extracted because they changed both the spatial and temporal treatments.

### 3.4. Alternate strategies

Of the 70 studies, 44 investigated the effects of multiple network management strategies, and only six compared alternate strategies with one another with respect to their effect on species viability. Four studies provide preliminary evidence that increasing turnover rate (i.e. the frequency at which a patch is subjected to turnover) can be compensated by (1) reducing turnover proportion (Ross et al., 2008; Wilcox et al., 2006), (2) increasing network area (Drechsler, 2011; Johst et al., 2011; Ross et al., 2008), (3) improving the habitat restoration rate (Johst et al., 2011; Wilcox et al., 2006), or (4) increasing network connectivity (only for species with high dispersal propensity; Johst et al., 2011). We will now provide more detailed explanations of the first three options, followed by a discussion of other alternate strategies that were investigated.

Reducing turnover proportion (i.e. the fraction of the network that is affected by turnover) was more effective than reducing the turnover rate (Ross et al., 2008; Ross et al. reduced turnover proportion by preventing habitat turnover in some patches (patch protection)). At low turnover rates, creating new patches was more effective (i.e.

increasing network area; see also the next paragraph), whereas at high turnover rates, protecting patches was more effective (Ross et al., 2008). At which turnover rate one strategy became more effective than the other depended on the specifics of the network and the species and on the assumptions regarding the financial costs of various actions, for which a generic threshold cannot be derived.

Reducing turnover proportion can buffer the impact of an increase in disturbance rate if the turnover proportion was initially high (Wilcox et al., 2006). When turnover proportion was low, increasing the habitat recovery rate was more effective at buffering an increase in disturbance rate (Wilcox et al., 2006). Increasing the patch creation rate was also effective compensating for increasing patch destruction at low levels of patch destruction, particularly for species with a high dispersal propensity and a low sensitivity to environmental stochasticity (Johst et al., 2011). In highly dynamic landscapes, reducing patch destruction was more effective than increasing the patch creation rate.

Increasing network area to alleviate the effects of increased turnover rates was possible for a range of species, and this strategy was particularly effective for species that are sensitive to environmental stochasticity (Johst et al., 2011). Drechsler (2011) identified trade-offs between network area and network turnover for a given budget, with the assumption that network area can be increased only when a larger turnover rate is allowed. Species with a high propensity for dispersion preferred larger, more dynamic networks, whereas species with a low propensity for dispersion performed better in smaller, more stable networks. When habitat restoration time was increased, the optimum performance shifted toward the smaller, more stable networks for all species. This shift is explained by the relatively lower amount of habitat that is available to species when restoration time is increased (see also Boughton and Malvadkar, 2002). A similar shift toward more stable networks occurred when habitat restoration was more expensive financially.

In both static and dynamic landscapes, increasing network area and increasing connectivity were effective alternate management options for species with a low propensity for dispersion (Johst et al., 2011). For species with a high propensity for dispersion, however, the specific network properties at hand determined if it was better to improve network connectivity or network area. In the successional landscape of Hodgson et al. (2009a), doubling the area of suitable habitat (increasing the network area) was most effective; however, if this was not feasible, it was better to concentrate patch management concentrated in a part of the landscape to create a smaller yet more compact network (increasing connectivity).

Vuilleumier et al. (2007) discussed some alternate management options, the effects of which depend on other network properties. These options include reducing the spatial correlation in disturbances, which was effective as long as the networks were not highly compact; in contrast, improving network connectivity and colonisation success were relevant regardless of the network structure.

#### 4. Discussion

We reviewed the knowledge base to determine whether the spatial and temporal properties of habitat networks can be changed to improve the viability of species in dynamic landscapes.

The 70 reviewed papers included both empirical and modelling studies and covered a wide range of species (Tables 1 and 2). From these papers, a picture emerges in which—in general—spatio-temporal dynamics in habitat networks negatively affect species viability relative to a landscape in which habitat suitability is static. These impacts may be compensated (at least to some extent) by managing the spatial and temporal properties of the network. However, knowledge regarding the impact of habitat turnover on network sustainability remains fairly incomplete and is too diverse to provide a quantitative evidence base for spatial planning.

However, it is possible to define qualitative planning guidelines for dynamic habitat networks. In the next sections, we will reflect on the results, identify knowledge gaps and research priorities and give a list of preliminary guidelines.

Spatial planning requires adapting both the spatial configuration and use of land units. Therefore, ecological studies that aim to provide guidelines for spatial planning must consider that ecological processes interact with the spatial parameters of the landscape. Current planning guidelines for ecosystem networks are based primarily on static network patterns. The presence of spatio-temporal habitat dynamics raises the following key questions: (1) which measures can compensate for reductions in network sustainability; (2) which measures are the most cost-effective; and (3) how much effort is required to adapt the network to meet conservation targets? Generally speaking, the following two generic strategies can be employed: managing the network pattern and managing the turnover regime.

##### 4.1. Managing the network pattern

All of the studies reviewed here support the notion that enlarging network area buffers the negative effects of habitat turnover. Preliminary indications suggest that the required increase in network size is in the order of 1.2–3.5 relative to static networks (Hinsch and Poethke, 2007; Johst et al., 2011). Further research is needed to adapt these results to other habitat turnover regimes. Increasing network connectivity was both empirically and theoretically shown to exert a clear positive effect on the persistence of a variety of species in dynamic landscapes. The magnitude of the effect is dependent on the level of spatial clustering in the turnover regime and species dispersal ability. Therefore, it is not possible to derive generic thresholds. An alternative to adding more patches to a network is to enlarge the existing patches. Current evidence suggests that enlarging the patches is the preferred strategy, but its effectiveness depends on the turnover rate. At a high rate of habitat turnover, populations become extinct due to habitat loss rather than to demographic stochasticity (see Section 3.2.3). As a consequence, the benefit of having large patches for large populations is lost, and in such a case, it may be more effective to have a higher number of smaller patches to distribute extinction risk across the network.

##### 4.2. Managing the turnover regime

Overall (i.e. in 74% of the studies), the viability of the species decreased with increasing habitat turnover. Species with high fecundity, strong dispersal propensity, strong intraspecific competition and a tendency for early-successional habitat were the most robust. However, even in cases in which habitat turnover yielded benefits to a species, increasing habitat turnover proportion potentially decreased the viability of that species (Groeneveld et al., 2008; Hodgson et al., 2009a). In general, species can cope with habitat turnover so long as the average patch life time is sufficiently longer than the species generation time such that individuals are able to reproduce and disperse before the habitat becomes unsuitable again. A substantial body of evidence suggests that clustered habitat loss should be avoided, whereas patch restoration has the most potential near large, occupied patches, at which colonisation probabilities are large. Furthermore, species perform better when habitat turnover is homogeneously distributed over time (i.e. relatively frequent yet small or mild impacts as opposed to infrequent yet large or intense impacts). This is an important result, given that climate change is expected to increase the frequency and amplitude of weather extremes (see also Jentsch et al., 2007). All of these generalities are in qualitative terms, and the studies that were reviewed preclude a determination of viability threshold levels. A set of general planning guidelines for

dynamic networks that emerged from our review are summarised in Box 1.

**Box 1** Qualitative planning guidelines for dynamic habitat networks. The number of studies that support the guideline relative to the total number of studies that investigated the strategy are given in parentheses. Note that the recommendations are scale-dependent.

#### Spatial network properties

- Enlarge network area (15/15).
  - Enlarging large patches is more effective than enlarging small patches (1/1; McCarthy and Lindenmayer, 1999).
  - To buffer against habitat turnover, 20–60% of a landscape should consist of habitat (4/4; Kallimanis et al., 2005; Keymer et al., 2000; Kun et al., 2009; Wimberly, 2006).
  - To achieve comparable species viability levels between static and dynamic networks, dynamic networks must be 1.2–3.5 times larger than static networks (2/2; Hinsch and Poethke, 2007; Johst et al., 2011).
- Increase network connectivity (14/15; e.g. Caruso et al., 2010; Johst et al., 2011; Magle et al., 2010; McCarthy and Lindenmayer, 2000).
  - For a given network area, see also Section 3.2.1.:
  - Networks with relatively few large patches may be preferred over networks with many small patches (8/11; e.g. Donner et al., 2010; McCarthy and Lindenmayer, 2000; Reed, 2004).
- Networks with patches of different sizes seem to be more robust than networks with equal-sized patches (2/3; DeWoody et al., 2005; Xu et al., 2006).

#### Temporal network properties

- Reduce the proportion of the network that is subject to turnover (10/13; e.g. Aviron et al., 2007; Groeneveld et al., 2008; Ross et al., 2008).
- It is better to disperse rather than aggregate patterns of patch destruction in space (13/18; e.g. Alados et al., 2009; Kallimanis et al., 2005; Reed, 2004) unless species are severely dispersal limited (2/18; Matlack and Leu, 2007; Wimberly, 2006).
- Conduct habitat restoration near source populations (3/3; Biedermann, 2004; Cornell and Ovaskainen, 2008; Wahlberg et al., 2002) and as quickly as possible (5/5; Drechsler, 2011; Ellner and Fussmann, 2003; Johst et al., 2011; Lowe, 2002; Wilcox et al., 2006).
- Reduce the turnover rate (30/42; e.g. Körner et al., 2010; Lundquist et al., 2010; Ranius, 2007; Snäll et al., 2005) unless species require a disturbance for habitat or life cycle events (5/35; e.g. Hinsch and Poethke, 2007; Menges and Quintana-Ascencio, 2004; Meulebrouck et al., 2009).
- Frequent yet mild disturbances are preferred over rare yet severe disturbances (3/3; Hinsch and Poethke, 2007; Robert et al., 2003; Stelter et al., 1997).
- It is preferred to distribute patch turnover homogeneously over time (3/3; (McCarthy and Lindenmayer, 2000; Menges and Quintana-Ascencio, 2004; Stelter et al., 1997).
- Reduce turnover intensity whenever possible (9/9; e.g. Bushing, 1997; Hinsch and Poethke, 2007; Tews et al., 2007).
- On average, patch life time should exceed species generation time (3/3; e.g. Hastings, 2003; Johnson, 2000b).

#### 4.3. Knowledge gaps and research priorities

Compared to the large body of work regarding static habitat networks and species viability, studies regarding dynamic networks are sparse. Although we screened 372 studies, the degree to which these studies allow conclusions that are relevant to spatial planning and the management of conservation networks is limited. Many studies failed to link with manageable features of the habitat network and focused primarily on evolutionary concerns such as the optimum levels of dispersal and fecundity. Although the potential scientific relevance of such studies cannot be denied, no planning guidelines can be derived from them.

The studies that we examined also precluded our ability to systematically compare multiple studies, for two reasons. First, the studies contained a wide variation in modelling frameworks and the metapopulation performance measures that were used. This variation severely complicated the comparison of these studies, as the results depend on the model's assumptions. Although different research questions can require different modelling frameworks, a standardised description of the framework that was used—for example, a description such as that suggested by Grimm et al. (2006)—would be helpful. Comparing results could also be facilitated by the standardisation of performance measures (e.g. measures presented by Drechsler and Johst (2010) and Grimm and Wissel (2004)). To further facilitate comparisons between studies, spatio-temporal habitat dynamics could be scaled to species and habitat characteristics. In this respect, we recommend scaling habitat life time relative to species generation time and scaling habitat network size and connectivity relative to species carrying capacity and dispersion (Kleyer et al., 2007; Vos et al., 2001).

From the current state of the art for modelling dynamic networks, only qualitative guidelines can be obtained (see Box 1); in contrast, planning requires quantitative information regarding effective measures, critical thresholds and relative cost-effectiveness. Our analysis revealed several important research gaps, and we propose that future studies should adopt the following research priorities:

- (1) Extend research towards network variables that have been studied relatively little (see Tables 1 and 2). A broad scientific basis will facilitate the understanding of the parameter interactions and will broaden the space for selecting effective conservation strategies in a dynamic world.
- (2) There seems to be a major lack of evidence to support critical thresholds in network sustainability in light of certain turnover regimes. In planning, it is of paramount importance to determine how much effort is required to effectively achieve particular conservation goals. A notable exception is Ross et al. (2008), who identified a threshold in patch disturbance probability of 0.08 per time interval. Below this threshold, it was more cost-effective to add patches; above this threshold, it was more cost-effective to protect existing patches. Considerably more attention should be paid to identifying critical thresholds for viability to provide an evidence base for decisions regarding the effort required to compensate for network dynamics.
- (3) Conservation planners and practitioners often must choose among alternate network management options. Unfortunately, only six studies explicitly compared alternate management options and could provide guidance regarding which options were more effective than others and under which conditions (Section 3.4). The inclusion of the financial costs of alternate actions in the analysis can provide further guidance regarding the trade-offs and cost-effectiveness of

alternate management options (see Drechsler, 2011; Hinsch and Poethke, 2007; Ross et al., 2008). Studies that compare particular turnover regimes and incorporate cost-effectiveness of alternatives would be extremely valuable for developing conservation planning strategies in a regional context.

- (4) The strong impact of species and habitat properties on planning recommendations is currently unclear. We recommend a systematic approach in which a range of species that vary in their life-history traits are included when testing the interactions between species viability and habitat turnover in habitat networks. In this approach, the concept of *ecoprofiles* (Opdam et al., 2008; Vos et al., 2001), which was developed for static networks, can be extended for dynamic networks by incorporating species variation in fecundity and longevity relative to habitat restoration time.
- (5) The effects of human-induced habitat turnover must be explored for a wider range of realistic habitat types that vary in their recovery time. Such an approach would lead to specific management recommendations for each type of ecosystem.

The role of spatial and temporal network properties for species viability in dynamic networks can only be studied properly if the total amount of habitat is kept constant. For this reason we excluded studies on the relation between species viability and habitat loss. However, the process of habitat loss is partly related to processes in habitat turnover, for which the large body of literature on habitat loss could be relevant for this work as well. While a full comparison is beyond the scope of this study, future work could explore these two fields. For example, one commonly studied threshold is the fraction of suitable habitat in the landscape that needs to remain to allow species to persist. This figure is generally known as 10–30% (e.g. Andr en, 1994; Swift and Hannon, 2010). Our results suggest that this figure may be twice as large for landscapes with habitat turnover (20–60%, Section 3.2.1).

#### 4.4. Habitat network dynamics as a management strategy?

Although the majority of the studies that we reviewed found that species respond negatively to habitat turnover, approximately 25% of the studies were either mixed or presented when and how habitat turnover can benefit a species (for example, in ecosystems that are driven by regular disturbances such as fire, inundation or mowing). In addition, note that we have focussed our review on single habitat-species interactions, excluding studies that examined how species interactions changed in the face of habitat dynamics. From the point of view of the intermediate disturbance hypothesis and community dynamics, the picture is likely to become more complicated (e.g. Kattwinkel et al., 2009; Turner, 2010). We found evidence that some degree of disturbance is beneficial for ecosystem types that thrive in the presence of regular disturbances.

Furthermore, spatial dynamics of habitat networks is not a matter of choice; rather, it exists in many parts of the world as a result of urban development and economically driven land use. Offset policies establish rules to compensate for this loss by restoring habitats elsewhere, which introduces spatial dynamics. Our review provides evidence for when and how these dynamics can be managed with the aim of improving the configuration of the network without sacrificing biodiversity in the long term. The insights that are summarised above suggest that networks can provide species with sustainable conditions while experiencing spatio-temporal changes, particularly in ecosystems in which species can tolerate such dynamics and provided the networks are sufficiently large and species response time well exceeds habitat turnover time. In addition, habitat restoration time should be considered.

Our study suggests that the negative effect of network dynamics can be mitigated to some extent by a range of measures (Box 1); however, several research gaps must be filled before more rigorous conclusions can be drawn. Nevertheless, in light of our findings, it is interesting to consider whether allowing spatial dynamics in habitat networks could be used as a conservation planning strategy, for example, to improve the network configuration or to make networks more resistant to either the dynamics of economic development or the effects of climate change. In geographical areas in which land use by humans has dominated the landscape and in which there is considerable fragmentation of the natural habitat, conservation networks are usually composed of the remaining natural or semi-natural patches, embedded in agricultural or urban landscapes. The spatial configuration of these patches is often sub-optimal. For example, in the Netherlands, following the first round of restoring the National Ecological Network, some provinces began to develop optimisation plans to improve the configuration. However, these optimisation plans did not incorporate the negative effects of habitat dynamics that are reviewed here, and they did not differentiate between ecosystem types.

With this review, we sought to provide a guide to conservation planners by reviewing the most readily available knowledge regarding species performance in dynamic habitat networks. Moreover, we identified knowledge gaps regarding the planning of dynamic habitat networks to help researchers design their future studies.

The majority of the studies in our review were modelling studies, which are a powerful instrument for exploring the potential future consequences of human-induced habitat turnover. However, both monitoring species trends in real landscapes and verifying assumptions in field experiments are essential to achieve effective conservation management. We hope that our review will be helpful for designing both types of studies in such a way that their results will be relevant to conservation planning in dynamic landscapes.

#### Acknowledgements

The authors thank the members of the EcoTRADE-project (<http://www.ecotrade.ufz.de>) for valuable discussions and Karin Johst, Mar Cabeza and various reviewers for their insightful comments on an earlier version of the manuscript. This research was funded through the ESF EuroDIVERSITY programme and the strategic research program “Sustainable spatial development of ecosystems, landscapes, seas and regions”, which is funded by the Dutch Ministry of Agriculture, Nature Conservation and Food Quality, and performed by Wageningen University and Research Centre. AvT was also supported by the Dutch “Knowledge for Climate programme”/CARE project and the FP7 EU project RESPONSES.

#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.05.001>.

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